Art. II.—*Contributions to our Knowledge of the Anatomy of Notoryctes typhlops, Stirling.*

Parts I. and II.

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(With Plates VI-IX.).

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Introduction.

The investigation, of which the following forms a record, has been carried on in the Biological Laboratory of the Melbourne University, for the use of which I have to thank Professor Spencer, who has also very generously placed his splendid stock of animals at my disposal, and has given me facilities in obtaining literature, some of which I might otherwise not have seen.

The subject matter falls naturally into three parts, each of which is complete in itself, though they are to a certain extent interrelated. Part III., on the Eye, is now ready for the press, an abstract of it having been read at the Dunedin Meeting of the Australasian Association for the Advancement of Science, in January, 1904.

Part I.—Nose, with Organ of Jacobson and Associated Parts.

Of the various structures to which of more recent years considerable attention has been directed, not the least interesting is the Organ of Jacobson, and with it the relations of the cartilages and bones of this region. Especially is this so in view of the valuable papers by Dr. Broom, on its comparative anatomy in the various groups of the Metatheria and Eutheria, in which he claims that, on account of the very slight tendency of these parts to vary with external variations, "we have a factor of considerable value in the classification of the Eutheria, probably of more value than either dentition or placentation." If this be so, and there seems strong evidence in its favour, we ought to find in this organ data on which to base a true conception of the relationships of such an aberrant form as Notoryctes, especially valuable since its embryology remains at present unknown. In itself a desirable result, this should also assist in defining the affinities of associated groups. Heretofore, apparently, nothing has been known of its structure in Notoryctes, nor even of its presence. This being so, it was suggested when working out the relations of the naso-lachrymal duct in connection with the eye, that I should include Jacobson's Organ in this research. Furthermore, we find that the structure and relations of the cartilages and bones associated with the nose are well worthy of record, as well as those of the organ itself.

In Broom's valuable thesis on Jacobson's Organ,[1] he has distinguished four types of this structure in mammals corresponding in part to the main groups: Monotreme, the most highly developed, Marsupial, Rodent, and general Eutherian; the main features of distinction being the character of the connection of the lumen of Jacobson's Organ with the naso-palatine canal, or with the nasal cavity, and the arrangement and degree of complexity of the cartilages. In view of the apparent value of this organ in classification, and the much modified character of Notoryctes, I have thought it desirable to make a more complete comparison of the various details of structure, with similar parts in other forms, than might have been necessary in some other animals.

Position of the Organ of Jacobson.

The organs of Jacobson are, as stated above, well developed in Notoryctes, being approximately equal in size to those of the Rabbit. They are situated near the floor of the nasal cavity, one on either side of the median line, just in front of the vertical plane of the osseous nasal septum, *i.e.*, 3.6 to 3.8 mm. from the anterior edge of the snout. They are separated from each other

1 Trans. Roy. Soc. Edin., vol. xxxix., 1898-1900, p. 234.

and partly enclosed by the bony palatine processes of the premaxillary bones (the prevomers of Broom) and by the cartilages of Jacobson. The Organ, with a small ledge of cartilage lying externally to it, causes an elongated triangular projection (Figs. 3, 4, 5, *i.s.r*) on the mesial wall of the nasal furrow, the base of the triangles being formed by the lateral wall of Jacobson's Organ. This ridge in the lining mucous membrane of the nasal furrow, which is always indicative in mammals of the position of this Organ, has been called by Broom "the inferior septal ridge." It is continued in a less degree anteriorly and posteriorly; anteriorly because of the presence of the cartilaginous shelf supporting the Organ, in front of the Organ itself, the trough so caused being here occupied by glands; while posteriorly the lower part of the ridge is still present, because of the bony shelf from the palatine processes of the premaxillary bones. Even where the Organ of Jacobson is itself present, the size of its consequent ridge is increased by a considerable development of glandular alveoli, outside Jacobson's cartilage and continuous with the gland masses in front of and behind Jacobson's Organ—compare Phascogale[1], Didelphys,[2] Perameles,[3] Pseudochirus.[4]

Cartilages and Bones in connection with the Nasal Organ.

The cartilaginous nasal septum (Figs. 1 and 2, *n.s.c.*) is present, dividing the nostrils right up to the anterior end of the snout. Its cartilage is hyaline, and the cells numerous, deeply staining and showing evidence of rapid growth.

As have others, we find that transverse vertical sections offer the best means of studying this part, aided also by longitudinal vertical sections. Beginning anteriorly, we find that the alinasal cartilage supporting each nostril is well developed, and is free anteriorly on its lower border (Fig. 1, *a.c.*), not being here united to the ventral processes of the septum, but swelling out instead into an edge which is club-shaped in transverse section, and supports a well marked ridge (*p.l.r.*), the cartilage being covered with a considerable thickness of gland material (*m.g.*), the whole rendering the cavity of the nostril crescentic in outline.

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1 Broom: Proc. Linn. Soc., N.S.W., vol. xxi., 1896, p. 593.

2 *Loc. cit.*, p. 597.

3 *Loc. cit.*, p. 599-600.

4 *Loc. cit.*, p. 603.

In outline the cartilages present in transverse section, that of an ornamental T. This ridge is referred to by Dr. Stirling[1], and is well shown in his accompanying figure of the animal. Dorsal to these alinasals lie the forward processes of the nasal bones (*n.b.*). Further back, the ridge containing the swollen edge of the alinasals, comes to lie more ventralwards, the superior position being taken by another ridge (Fig. 5, *s.l.r.*) with glandular interior, and containing a large duct from the mucous glands posterior to this level. A short distance behind the beginning of the second ridge there arises a process from the arch of the alinasal cartilage on each side, connecting each with one of the ventral processes of the nasal septum (*n.f.c.*), so that at this point, and not anterior to it, the nostril is completely enclosed on each side with cartilage. This condition is closely comparable with that in Macroscelides, as shown in the figures given by Broom[2]. Soon there pierces the alinasal cartilages a canal on each side, through which passes one of the naso-lachrymal ducts, which open in front of this, on the ventral surface of the primary lateral ridge into the ventral nasal furrow (*v.n.f.*) on each side. Between the plane of the opening of the naso-lachrymal duct, and that of its passage through the encircling cartilage, I have been able to trace a splitting off from the ventral surface of the cartilage of the nasal floor (formed by ventral processes from the cartilaginous septum), of what is at first a thin lamella of cartilage, in three parts. Those on either side lose their connections with the nasal floor except for a while at the extreme outer edge of each, and finally become continuous with the anterior edge of each premaxillary bone. The central portion remains longer in connection with the nasal cartilage, so that, in a transverse section taken just at the level of the passage of the naso-lachrymal ducts through the alinasal cartilages, the following relations exist. The nasal septum (Fig. 1, *n.s.c.*) is very thin and deep, giving off above the two alinasal cartilages (*a.c.*), and ventrally two processes (*n.f.c.*) forming the floor of the nasal cavity. Compare in this respect Ornithorhynchus, in which the nasal septum becomes united with these nasal floor cartilages.[3] This is to be

1 Stirling: Trans. Roy. Soc. S. Aus., 1891, p. 159, pl. iii.
2 Proc. Zool. Soc. Lond, 1902, vol. i., pl. xxi., fig. 1.
3 Broom: Trans. Roy. Soc. Edin., vol. xxxix., p. 235.

contrasted with the condition found in most Marsupials, and also in Rodents, in which they are at most in contact with the nasal septum. In the Macropodidae, Symington[1] has noted the connection of the nasal floor cartilages to the ventral edge of the nasal septum, by perichondrium.

Beneath this, and separated from the cartilage by connective tissue and blood-vessels, are the extreme anterior ends of the premaxillary bones (*p.b*), just losing their fibrous cartilaginous connections with the lateral edges of the nasal floor, and separated from each other in the middle line by a large vein (*v.*). Above this vein is a somewhat wedge-shaped nodule of hyaline cartilage (*p.c.*), which in the next section posteriorly sends down a fibrous process to occupy the space between the two premaxillaries, pushing the vein ventralwards. In this section, also, the nasal bones (*n.b.*) have grown down, enclosing the alinasal cartilages nearly to the level of the primary ridge, and three sections further back the nasal and upward processes of the premaxillary bones meet, completing the bony as well as the cartilaginous capsules round the nose. Still proceeding backwards, we find that the wedge-shaped cartilage has now completely descended between the premaxillaries to form the connection between their mesial edges. The above description can be readily corroborated on reference to longitudinal sections. Splitting off anteriorly from the ventral edge of the septum is the narrow sheet of fibrous cartilage passing obliquely downwards and backwards to lie between the palatal processes of the premaxillary bones in their anterior part. On the hinder face of this sheet of cartilage is the hyaline cartilaginous swelling, which in transverse section appears wedge-shaped. In front of the sheet, the bones are separated by a well-defined vein, connected with a large blood sinus, which curves round vertically in front of the cartilaginous septum. Posteriorly in these longitudinal sections we can see that the central cartilaginous bar or narrow sheet becomes lost as the two palatal processes of the premaxillae become more intimately united. There can be, I think, no doubt but that this central cartilage represents here the prenasal cartilage of other animals. Its general

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1 Jour. Anat. and Phys., vol. 26, p. 372, and pl. x., fig. 1.

relations greatly resemble those shown by Broom to exist in the foetal calf.[1] With reference to the transverse plates of cartilage described by Broom as existing on each of the central rod, and supporting the papilla between the naso-palatine canals, which is so marked in Marsupials,[2] such for example as in Didelphys murina,[3] in Perameles nasuta,[4] in Petaurus,[5] and Trichosurus,[6] Phascolomys[7] and Macropus.[8] I can find no trace of hyaline cartilage in such a position, but the fibrous sheet of cartilage which connects the main part of this prenasal between the premaxillary processes with the nasal septum, sends out laterally a thin ill-defined fibrous layer (Figs. 2 and 3, *f.p.c.*), which extends backwards beneath the palatal processes into the papilla, behind which it does not exist. Apparently this represents the papillary cartilage of other Marsupials, and that of Miniopterus[9] and Macroscelides.[10]

Returning to the vertical transverse sections, we find that not only the primary and secondary lateral ridges, but also the septal cartilage are covered by a great thickness of glandular alveoli, forming on the septum the superior septal ridge (*s.s.r.*). These glands have well defined ducts, often .06 mm. in diameter, running longitudinally, to open far forwards into the vestibule. The thickness of the glandular layer varies on the superior septal ridge .24 to .52 mm., and on the superior lateral ridge .24 to .6 mm. The lining membrane of the nasal cavity over these ridges is smooth, like that of the Guinea-pig, and so unlike that of the Rabbit, which is much plicated. About this vertical plane, the cartilaginous projection, supporting the primary ridge from the lateral wall, diminishes greatly in size and finally disappears, so that on each side the cartilages of the nasal floor now form a very shallow double U-shaped curve, each of the nasal furrows of each side occupying the loop of one U, the mesial edge of the

1 Proc. Linn. Soc. N.S.W., vol. x., n.s., pl. xliv., fig. 7, and p. 561.

2 *Loc. cit.*, fig. 6, and p. 560.

3 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, p. 597.

4 *Loc. cit.*, p. 599.

5 *Loc. cit.*, p. 604.

6 *Loc. cit.*, p. 607.

7 *Loc. cit.*, p. 613.

8 *Loc. cit.*, p. 610.

9 *Loc. cit.*, vol. x., n.s., 1895, pl. xliv., figs. 4, 5, p. 560.

10 Proc. Zool. Soc. Lond., 1902, vol. i., pl. xxi., figs. 8, 10, p. 226.

inner U being continuous with the ventral edge of the nasal septum, while the naso-lachrymal duct lies underneath in the angle formed between the two loops. The arrangement of this double U-shaped cartilage, and the subsequent reduction of the cartilages (to be immediately described in Notoryctes), may be compared with that shown in Klein's figures of the Guinea-pig,[1] though here the central cartilage is not connected with the septum as it is in Notoryctes. Gradually here the outer U becomes lost on each side at about the level of Stenson's duct, or a little posterior to that duct. Compare this with Didelphys murina,[2] Perameles,[3] Aepyprymnus,[4] and contrast with Trichosurus.[5] In Notoryctes, however, this outer cartilage is present behind the naso-palatine canal as a rudiment. At the same time, the alinasal cartilages, having receded dorsally, only extend down in the upper third of the nasal wall. At this point, each nasal cavity (Fig. 2, *n.c.*) in transverse section resembles a two-pronged fork, the two prongs being represented by the two nasal furrows (*v.n.f.*).

A change is also noticeable in the outlines of the palatal processes of the premaxillae, which are still united only by the median cartilage above described. The adjacent edges of the premaxillaries, which are thin anteriorly, become much thickened posteriorly (Fig. 2, *p.p.p.*), wedge-shaped in cross section, their mesial faces being convex to each other. The upper edge of this wedge now becomes more marked, rising up in a crescentic fashion (compare especially Phascolgale[6], in which, however, they are much smaller than in Notoryctes and Perameles[7]), till it touches the ventral cartilage of the nasal floor, the lower edge of the wedge disappearing. In this plane (Fig. 2, *J.c.*) there appears a swelling in the hyaline cartilage of the nasal floor, from which passes back a bar, also of hyaline cartilage, part of Jacobson's cartilage. The swelling in the mesial wall of the ventral nasal furrow, *i.e.*, the inferior septal ridge (*i.s.r.*), caused by the cartilage,

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1 Quart. Jour. Micro. Science, vol. xxi., pl. xvi., fig. 1, 2, 3.

2 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, p. 597.

3 *Loc. cit.*, p. 601.

4 *Loc. cit.*, p. 610.

5 *Loc. cit.*, p. 607.

6 *Loc. cit.*, p. 593.

7 *Loc. cit.*, p. 599.

and which increases in size greatly and almost immediately, occasions a pushing in of the ventral nasal furrow, the cavity of which now becomes in cross-section foot-shaped, the inferior septal ridge filling up the instep. Suddenly, just posterior to this, there appears the swollen anterior end of Jacobson's Organ (Fig. 3, *J.O.*). The cartilage of the nasal floor may be now called in part Jacobson's cartilage, since it has here lost its connection with the nasal septum (Fig. 3, *J.c.*). In this respect Notoryctes resembles Ornithorhynchus[1] and Echidna,[2] in which Jacobson's cartilage "is continuous in front of the naso-palatine foramen with the cartilage in the floor of the nose," as also with the septum, "while behind it is separate." It resembles also the Rabbit,[3] and also the Guinea-pig,[4] in that the cartilage is continuous with the cartilage of the nasal floor, though in each of the latter the cartilage of Jacobson is altogether independent of the cartilaginous nasal septum. The cartilage of Jacobson now consists, on each side, of a crescentic shelf, from the middle of the concavity of which rises, at right angles, a band of cartilage (*o.J.c.*), under which runs, near its anterior end, Jacobson's duct (Fig. 3, *J.d.*) into the "toe" of the nasal furrow, while in the groove formed between the band and the upper horn of the crescent lies the Organ of Jacobson. In Notoryctes, the crescentic cartilage of Jacobson is oblique, similar to that of Petaurus[5], and unlike that of Pseudochirus and Petauroides[6], which are more vertical.

The band or shelf of cartilage supporting the lateral wall of Jacobson's Organ, is comparable in part to what is called the septal turbinal in Macroscelides,[7] though arising from the main cartilage at a different angle. It is further comparable to Macroscelides in that this shelf is only connected with the ventral cartilage behind the exit of Jacobson's duct from the Organ, near its anterior end. This outer bar is similarly found in most Marsupials, but that in Notoryctes differs from them in

1 Proc. Zool. Soc., 1891, p. 578.
2 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, p. 592.
3 Q.J.M.S., vol. xxi., p. 550.
4 *Loc. cit.*, p. 220.
5 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, p. 604.
6 *Loc. cit.*, p. 604.
7 Proc. Zool. Soc., vol. i., pl. xxi., figs. 3 and 4, p. 226.

one particular, viz., that in them this bar is connected above and in front with the upper end of Jacobson's cartilage, and below and behind with its lower outer edge. In Petaurus,[1] however, and Phalangers,[2] and to a less extent in Trichosurus[3] and Macropods,[4] there is a ridge process exactly similar to that of Notoryctes in its origin from the inner upper side of Jacobson's cartilage, becoming detached from it, and then more posteriorly becoming attached to the lower ridge of the cartilage. The "bar" in Notoryctes apparently truly corresponds to that of the other marsupials in that it comes off anteriorly to Jacobson's duct from the ridge process, curls round the Organ and over the duct, and becomes attached posteriorly to the duct, to the ventral edge of Jacobson's cartilage, being therefore merely a further exaggeration of what is present in Petaurus, and the Phalangers generally. Meanwhile in Notoryctes, the cartilaginous connection between the palatine processes of the premaxillaries has almost disappeared, the two bones by this time practically fusing. The crescentic character of the bones now harmonises closely with that of the cartilages (Figs. 3 and 4, *p.p.p.* and *J.c.*). From the ventral convex surface of the rapidly dwindling cartilage of the outer nasal floor, is given out just here a small process of hyaline cartilage (Fig. 3, *s.c.*), which is found strengthening the upper and anterior wall of Stenson's duct which lies just posterior to this. Here we have another point of difference from other Marsupials, in which there is no cartilaginous support to the naso-palatine canal, though in Petaurus[5] and others we find a process supporting the inner wall. This may also be compared with the Rabbit,[6] in which Stenson's cartilage is a continuation from the cartilage of the nasal floor, and contrasted with the Guinea-pig,[7] in which the cartilage forms a closed capsule around the two ducts, and is quite separated from all other cartilages. It is to be noticed here, that the upper horn of the crescentic Jacobson's cartilage is

1 Proc. Linn. Soc. N.S.W., vol. xi. n.s., 1896, p. 604, pl. xliv., figs. 10, 11.

2 *Loc. cit.*, p. 616.

3 *Loc. cit.*, p. 607.

4 *Loc. cit.*, p. 618.

5 Broom: Trans. Roy. Soc. Edin., xxxix., p. 240.

6 Klein: Q.J.M.S., vol. xxi., p. 555.

7 *Loc. cit.*, p. 228.

thinning out greatly, as also the cartilage underlying the ventral nasal furrow, so that, about the level of the exit of Stenson's duct from the nasal furrow, there is no cartilage left in this region, except for remnants of the outer nasal floor cartilage (Fig. 4, *n.f.c.*), and the outer bar of Jacobson's cartilage (*o.J.b.*). Thus, here the median and lower lateral parts of the cartilaginous crescent disappear first as compared with the Rabbit,[1] and, contrasted with the Guinea-pig,[2] the upper lateral or lower lateral parts of which go first. At first this remnant of cartilage appears to become directly connected by its perichondrium with the lower edge of the crescentic bone (Fig. 5) as found by Klein in the Guinea-pig; soon the cartilage disappears altogether, leaving a very thin bony shelf (Fig. 5, *p.p.s.*) in its place. Compare this with Perameles,[3] and also with the Macropodidae[4] in so far that the cartilages of Jacobson form an incomplete tube, becoming reduced posteriorly. At this level, nerve fibres occupy almost the whole space between the bone and the mesial wall of the Organ.

Posterior to the Organ of Jacobson the inferior septal ridge still remains because of the persistence of the bony shelf, which anteriorly helped to support Jacobson's Organ; while, as far forward as the anterior end of the Organ, the primary lateral ridge (*p.l.r.*), which has been for a short distance devoid of special support, is invaded by a thin lamina of bone from the maxillary bone, becoming the maxillo-turbinal (*m.t.*). In the hinder part of this region the palatal processes are overlain in the middle line by the anterior portion of the vomer, so that there is now a complete bony partition between the right and left nasal cavities, from dorsal to ventral or palatal surfaces.

Ducts of Jacobson and of Stenson.

The duct connecting the lumen of Jacobson's Organ with the nasal cavity (Fig. 3, *J.d.*) is very short, .06 mm., since the wall enclosing the ventral sulcus of the extreme anterior end of the Organ lies almost immediately in contact with the mesial edge,

1 Klein: Q.J.M.S., vol. xxi., p. 554.
2 *Loc. cit.*, pl. vii., fig. 2.
3 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, p. 600, fig. 8.
4 Jour. Anat. and Phys., vol. 26, p. 372.

which is also the most ventral part of the nasal furrow (*v.n.f.*). The duct then passes outwards almost horizontally to open into the nasal furrow. At this plane, in transverse sections, is also seen the external aperture of the naso-palatine, or Stenson's duct (Fig. 3, *n.p.d.*), into the mouth. This duct, which is .40 mm. long, runs inwards, upwards, and backwards, piercing between the premaxillae and palatine processes to its origin from the ventral edge of the nasal furrow, some distance behind the opening of Jacobson's duct into it (Fig. 4, *n.p.d.*). There is, therefore, no direct communication between the cavity of the Organ and Stenson's duct, except through the cavity of the nasal furrow; this is confirmed by the difference in structure between the wall of Jacobson's duct and of Stenson's duct, and the intervening nasal furrow.

This condition may be compared with that described by Broom as an exception among Marsupials in Aepyprymnus[1], by Klein in the Guinea-pig[2] and Rabbit,[3] by Harvey in the Rat and Hedgehog,[4] and by Broom in Dasypus.[5] It may also be contrasted with that in Ornithorhynchus[6] and Dog,[7] and the usual Marsupial and higher Mammalian types, as described by Jacobson, Gratiolet, Balogh, Fleischer, and Broom, in which Jacobson's Organ opens into Stenson's duct, otherwise remaining closed, *e.g.*, in Macropus[8], Phascologale[9], Dasyurus[10], Didelphys[11], Perameles[12], and Phascolomys.[13] The openings of Stenson's ducts into the mouth cavity are separated by a well-marked papilla, the centre of which becomes somewhat hollowed out (Fig. 3). This, as stated above, is supported, anteriorly at least, by a fibrous continuation from the prenasal cartilage (*f.p.c.*). The similarity of the general relations of the parts seen in such a section of Aepyprymnus as

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1 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, p. 610.
2 Q.J.M.S., vol. xxi., p. 219.
3 *Loc. cit.*, p. 555-6.
4 Q.J.M.S., vol. xxii., p. 50.
5 Trans. Roy. Soc. Edin., vol. xxxix., p. 242.
6 Proc. Zool. Soc. Lond., 1891, p. 578.
7 Q.J.M.S., vol. xxii., p. 301-2.
8 Jour. Anat. and Phys., vol. xxvi., p. 372.
9 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, p. 593.
10 *Loc. cit.*, p. 594.
11 *Loc. cit.*, p. 597.
12 *Loc. cit.*, p. 600.
13 *Loc. cit.*, p. 613.

that shown by Broom[1] to those seen in a similar section of Notoryctes is considerable, especially in reference to Jacobson's cartilage, the opening of the duct into the nasal cavity, and its relation in vertical plane to the dorsal opening of the naso-palatine duct into the nasal furrow, and to its ventral opening into the mouth.

General Structure of Jacobson's Organ.

As in the Organ of Jacobson previously described in other animals, the lumen of the tube (Figs. 3, 4, 5, *J.O.*) in Notoryctes is more or less laterally compressed in its main portion, so that we distinguish the lateral (*l.w.*) and median walls (Fig. 6, *m.w.*), which meet at the upper and lower sulci. In the examples of which I have sections, the left tube is greater in vertical diameter than is the right, the latter, moreover, in great part of its length being almost circular, while, right to the hinder end, the left organ retains, in an increasingly marked manner, its compressed character, its cavity being posteriorly a mere slit. As usual, the sensory epithelium is confined more or less strictly to the median wall. In shape this Organ is generally speaking oval, but much drawn out and bluntly pointed posteriorly, while anteriorly it often ends quite abruptly. The length of its lumen is 1.2 mm., its total length being 1.4 mm. Its ventral edge is almost straight, the dorsal edge curving downwards posteriorly to meet the former. Its outline in transverse section varies considerably. Posteriorly, it is much flattened from side to side, its lateral wall being in parts slightly indented, though it can scarcely be called kidney-shaped (Figs. 5 and 6, *J.O.*). This to a certain extent is comparable with that shown for part of the Organ in Miniopterus,[2] by Broom, by Klein in the Dog,[3] and in a much less degree with that shown by Symington and Smith, in Ornithorhynchus[4] and Echidna,[5] and by Broom in marsupials generally. But, whereas in the former of these it is due more or less to an incurving of Jacobson's cartilage, in Notoryctes it is simply due to a thickening of the subepithelial

1 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, pl. xlvii., fig. 11.

2 Proc. Linn. Soc. N.S.W., vol. x. n.s., 1895, pl. 47, fig. 4.

3 Q.J.M.S., vol. xxii., p. 305.

4 Proc. Zool. Soc., 1891, p. 579.

5 Anat. Anz. XI. Band., 6, 1895, p. 162-3.

layers of the lateral wall, there being no inturning of the capsule. In the Rabbit[1] and Marsupials, however, there is a similar somewhat kidney-shape in the central portion of the Organ, due only to subepithelial and glandular thickening. This indentation, moreover, is not constant, as, occasionally, as above stated, while one side retains more or less of the concavity in its lateral wall, the Organ of the other side may be quite oval or even circular in transverse outline.

In vertical diameter the Organ varies from .32 to .6 mm. Horizontal diameter, .12 to .28, very slightly less than in the Rabbit, and slightly under half of that of the Dog and Guinea-pig. Into the upper and lower sulci of the Organ there open a considerable number of ducts from the gland mass on either side of the nasal septum. Seven or eight of such ducts may at times be seen in one single longitudinal section opening into the upper or dorsal sulcus, and a lesser number into the ventral sulcus. These ducts, which are short, wide, and have darkly staining walls, lie at right angles to those from the same gland mass, which run forwards longitudinally, and more or less parallel, till they open into the vestibule close to the external orifice. The latter longitudinal ducts are usually fifteen to twenty in number on each side of the cartilaginous septum.

Blood Vessels.

Jacobson's Organ is well supplied with these (Figs. 5 and 6, *v.*, *a.*, *ct.*). Alongside its lateral wall, there run an artery and two veins, the former curving round anteriorly, from dorsal to ventral surfaces, and between the front end of the Organ and its supporting cartilage in this region, while both laterally and ventrally in the median wall is to be found a more or less extensive plexus of blood vessels (Figs. 5, 6, *c.t.*).

Nerves.

In longitudinal sections, especially, there is to be noted a large branch of the olfactory nerve passing forward horizontally and entering into relation with the dorsal and mesial surfaces of the

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1 Q.J.M.S., vol. xxi., p. 558.

posterior part of the Organ, descending anteriorly to the mesial wall, as seen in transverse sections (Fig. 6, *n.f.*).

Minute Structure of Jacobson's Organ.

For convenience of description we may take first the lateral wall, with the structures outside this, and then similarly the median wall.

1.—The Lateral Wall.

The epithelium lining the Organ of Jacobson on this side (Fig. 6, *l.w.*) is .04 to .06 mm. thick, being slightly less than in the Dog, and the same as in the Guinea-pig and Rabbit. It consists of a columnar epithelium, similar to that lining the nasal cavity (which is .06 mm. thick), having here apparently two layers of cells; (*a*) an outer columnar layer with long, strong cilia (*c.f.*, Guinea-pig and Dog, and contrast the Rabbit), and oval nuclei. These are interspersed with goblet cells, which are numerous in parts of the lower half of the wall; (*β*) an inner layer with rounded nuclei. It will be seen that this differs from that of the Guinea-pig as described by Klein[1] in that his middle layer of spindle-shaped cells is not visible here. Probably this is due to the fact that all the material at my disposal is spirit-hardened, and in such cases Klein has found great difficulty in distinguishing the spindle-shaped cells from those of the columnar layer. Next to this is a well-marked fibrous layer corresponding to the subepithelial layer of other forms, with blood vessels and gland alveoli. The cavernous tissue shown by Klein to be so well developed in this position in the Guinea-pig[1] and Rabbit,[2] and by Broom in Phascolarctos,[3] and in Petauroides,[4] does not exist here in Notoryctes, the blood vessels of this side being limited to an artery (*a*), running longitudinally along the middle line of the tube, and one or two small veins. This is more like what we find in the ordinary Marsupials, which have a single hilar blood vessel. It may be seen in Macroscelides,[5] and is much greater in extent than in the lateral wall of

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1 Q.J.M.S., vol. xxi., p. 101-3.

2 *Loc. cit.* p. 563-4.

3 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, p. 613.

4 *Loc. cit.*, p. 607.

5 Proc. Zool. Soc., 1902, vol. i., p. 226.

Miniopterus.[1] The glandular development is here (*m.g.*), as in the Rabbit,[2] and, contrasted with Miniopterus[1] and the Guinea-pig, most marked in the cartilaginous capsule, at the upper and outer part of the Organ, though unlike the Guinea-pig, where the glands are more numerous when the cartilage is absent, in Notoryctes there seems to be no such invariable relation. There are also, as described above, numerous glands lying in the inferior septal ridge (*i.s.r.*) outside Jacobson's cartilage. In this respect, Notoryctes agrees with Didelphys murina,[4] Trichosurus,[5] and Dasyurus maculatus,[6] while differing from the Phalangers generally, and from Perameles[7] and Dasyurus viverrinus.[8] At the same time, we find the general Diprotodont feature, characteristic also of Phascolomys,[9] in which numerous gland ducts open into the Organ from above. With regard to these glands around Jacobson's Organ, it may be remarked that they appear to be regarded by Klein, as also those on the septum, as true serous glands in the Rabbit[10] and Dog;[11] while Broom finds, in the septum, mucous glands in Miniopterus,[1] and in various Marsupials also.[12] In Notoryctes, those in the mucous membrane of the septum and ridges covering the turbinal bones, appear to be true mucous glands, though those around the Organ of Jacobson and a small group on each side of the bottom of the nasal septum are apparently serous in character, and have smaller alveoli, more deeply staining nuclei, broader, deeply staining ducts, which all open into Jacobson's Organ. The gland ducts chiefly enter the tube at the upper and lower sulci, though occasionally they open through the lateral wall itself as previously found in the Rabbit[10] and Sheep. Their number would account for the fact that the tube is always

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1 Proc. Linn Soc. N.S.W., vol. x., n.s., 1895, p. 574.
2 Q.J.M.S., vol. xxi., pp. 563-4.
3 *Loc. cit.*, p. 103.
4 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, p. 598.
5 *Loc. cit.*, p. 607.
6 *Loc. cit.*, p. 596.
7 *Loc. cit.*, p. 602.
8 *Loc. cit.*, p. 596.
9 *Loc. cit.*, p. 613.
10 Q.J.M.S., vol. xxi., p. 564.
11 *Loc. cit.*, vol. xxii., p. 306.
12 *Loc. cit.*, vol. xi. n.s., 1896, p. 614; Trans. Roy. Soc. Edin., vol. xxxix., p. 233.

full of secretion. From this, as from the large size of the Organ, we may perhaps infer that in Notoryctes the glandular function is relatively more important than the sensory one.

Coming down from the side of the septum, and running longitudinally, are a small number of scattered nerve fibres similar to those described by Klein in the Rabbit.[1]

The main features of the histology also agree closely with those described by Symington in Macropodidae.[2]

2.—Median Wall.

The sensory epithelium lining this wall (Fig. 6, *m.m.*) extends also as described in the Guinea-pig by Klein[1] in the anterior half, a short distance down the lateral wall of the superior sulcus, but ending at the angle of the inferior sulcus for the whole length. Its thickness varies from .08 to .1 mm., slightly greater than in Dog, and slightly less than the Guinea-pig. In the posterior part the sensory epithelium ends also at the angle of the superior sulcus. The boundary between the epithelium of the lateral wall and the sensory epithelium of the median wall is always very sharply marked off.

The sensory epithelium in Notoryctes resembles closely in its general structure that of the Guinea-pig,[3] Rabbit[4] and Dog,[5] though the minute structure of the cells cannot be made out in these spirit specimens. The epithelial cells which bear short cilia appear much longer and thinner than those of the lateral wall, and have a striated border, probably due to the terminal rods of the cells in the lower layer. These epithelial cells have oval nuclei, which are disposed in three ill-defined layers similarly to the above mentioned forms. The sensory cells have large spherical nuclei more transparent and less deeply staining with haematoxylin, and with a well-marked nuclear membrane and network. They are arranged in one or two layers (as in the Dog), usually in one layer near the upper and lower sulci, and two layers in the median part of the wall. In one or two places

1 Q.J.M S., vol. xxi., pp. 556, 564.
2 Jour. Anat. and Phys., vol. xxvi., p. 373.
3 Q.J.M.S., vol. xxi., p. 105-6.
4 *Loc. cit.*, p. 564, etc.
5 *Loc. cit.*, vol. xxii., p. 307-310.

in the length of this wall, the gland ducts pass through to open into the tube, the last part of their wall being lined by a continuation of the sensory epithelium.

The space between the Organ of Jacobson and the cartilage of Jacobson, or the bone of the crista nasalis, is closely packed in its upper half with nerve fibres (Fig. 6, *n.f.*). These are much more numerous in the median and posterior portion of the wall, decreasing in quantity anteriorly. At the hinder end of the tube, a large bundle passes off to run in the septal mucous membrane until finally it joins the main olfactory trunk. I have been able to trace these fibres among the cells of the sensory layer, but not actually into the cells, where doubtless they do end. As the nerve fibres decrease in number their place is taken by glands. The cavernous tissue (*c.t.*) so conspicuous in Klein's figures of the *lateral* wall in the Guinea-pig[1] and Rabbit,[2] and much more rudimentary in the *median* wall of the Dog,[3] is very abundant in the lower half of the median wall in Notoryctes. Here there are one or two arteries and several somewhat large veins forming a plexus, and supported by ordinary loose fibrous tissue. In the position of the nerves and veins in this median wall, we may compare this with Phascolomys.[4] In Notoryctes, as previously stated, the distinction between the medial and the lateral epithelium persists right to the posterior end of the Organ, as contrasted with the Rabbit, where only columnar epithelium is found at the posterior end of the Organ, and with Phascologale[5] and with Macroscelides.[6]

Jacobson's duct, as heretofore described, is extremely short, and is lined by a continuation of the ordinary nasal epithelium similar to that of the lateral wall. This is to be contrasted with the ordinary marsupial, *e.g.*, Dasyurus,[7] in which Jacobson's duct is lined with squamous epithelium.

Stenson's duct, however, is lined by stratified pavement epithelium continuous with that lining the palate. The surface

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1 Q.J.M.S., vol. xxi., pl. vii., fig. 5, pl. xvii., fig. 6.
2 *Loc. cit.*, pl. xxx., fig. 5-8.
3 *Loc. cit.*, vol. xxii., pl. xxvi., figs, 14, 15.
4 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, 614.
5 Proc. Linn. Soc. N.S,W., vol. xi., n.s., p. 594.
6 Proc. Zool. Soc., 1902, vol. i., p. 226.
7 Proc. Linn. Soc. N.S.W., vol. xi., n.s., 1896, p. 595.

layers of the lining of the duct are strongly corneous, this diminishing, as in the Dog,[1] as it enters the nasal furrow, to one-third of its thickness on the palate. The bottom of the furrow near Stenson's opening is similar to that of the duct itself. There are no glands opening through the wall into the canal of Stenson, as found in the Sheep (Balogh) and Man (Kolliker), but which Klein was unable to find in the Guinea-pig.[2]

It is worthy of note that the stratified pavement epithelium lining the vestibule of the nose, which may be up to .1 mm. thick, has a very thick corneous layer which may be in itself .04 mm. thick, the epithelium covering the snout itself being up to .25 mm. in thickness, of which the corneous layer makes up .1 mm.

Summary and Relations to other Forms.

The chief points[3] to be considered in discussing the relations of the Organ of Jacobson in Notoryctes to that of other forms are: (1) the direct or indirect connection of Jacobson's duct with the naso-palatine or Stenson's duct; (2) the presence of the outer bar of Jacobson's cartilage; (3) the presence or otherwise of a cartilaginous bar of support for the naso-palatine canal; (4) presence or otherwise of the outer nasal floor cartilages behind the naso-palatine canal; (5) the papillary cartilage of the prenasal cartilage; (6) the arrangement of the blood vessels.

I.—Jacobson's Duct, in Notoryctes, is seen clearly to open directly into the nasal furrow, from which in turn Stenson's duct leads down to the oral cavity. Here then we have the structure regarded by Broom as typical of the Rodents,[4] and also found by him in one Diprotodont form Aepyprymnus, and in Dasypus among the Edentata. In reference to this feature in Aepyprymnus[5], Broom considers it to be only a slight difference in the relative position of these openings, "due to the lengthening of the front of the snout in connection with the well-developed front incisors." But it cannot be so caused here in Notoryctes,

1 Q.J.M.S., vol. xxii., p. 301.

2 Q.J.M.S., vol. xxi., p. 229.

3 *c.f.*, Broom: Proc. Zool. Soc. of London, 1902, vol. i., pt. ii., p. 226.

4 Proc. Linn. Soc. N.S.W., vol. x., n.s., 1895, p. 572.

5 *Loc. cit.*, vol. xi., 1896, p. 619, and Trans. Roy. Soc. Edin., vol. xxxix., p. 241.

and one is led to think that there is more meaning in its presence there also, than that of mere parallel development in two animals possessing a rodent type of dentition, even if, as stated by Broom,[1] we are to regard Aepyprymnus as "approximating to a rodent type of dentition."

II.—We have seen that in Notoryctes, for a part of the length of its lateral wall, it has a more or less convex character, so constricting the lumen of the Organ, this being due, not to a well marked cartilaginous support as in Ornithorhynchus, or to an incurving of the edge of the cartilage as in Echidna, or even in Miniopterus or the Dog, but to a thickening of the subepithelial and glandular layers of the lateral wall, forming a "gland fold," as in the Rabbit and Guinea-pig, and in its near allies, the Marsupials. Also we find in this lateral wall the outer bar of Jacobson's cartilage as a ridge process, which is undoubtedly the rudimentary homologue of the turbinal found in the more highly organised structure of Ornithorhynchus, and to a less extent in Echidna. In a more or less developed form this outer bar is found in all Marsupials. In the degree of development found here, Notoryctes is most closely allied with the Phalangers, especially Petaurus in which it is more developed than in the Polyprotodont Dasyure, and with the Macropods to a less extent, and with Dasypus and the Rodentia among the Eutheria.

III.—The cartilaginous support for the naso-palatine canal in marsupials is never more than rudimentary; and even so, as in Perameles, Trichosurus, Phascolarctus, Macropus, Phascolomys, and Petaurus, it is always on the inner side and not on the outer anterior side of the canal, as in Notoryctes; and also in the Rodents, in which, however, it is much larger than that in Notoryctes, and in Miniopterus among the Cheiroptera.

IV.—In Notoryctes, as slightly different from other Marsupials, and Edentates, there is a very fragmentary continuation of the hinder edge of the outer nasal floor cartilages for a short distance behind the opening of the naso-palatine canal. In a degree, this may indicate a leading-on to the Rodent type, in which the cartilage persists behind the plane of the naso-palatine canal.

It must be remembered here, also, that in the attachment of the

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1 Trans. Roy. Soc. Edin., vol. xxxix., p. 241.

nasal floor cartilages anteriorly to the septum, we find a similar condition in Ornithorhynchus and Echidna only.

V.—Though not developed to nearly the same extent that it is in Ornithorhynchus, or Echidna, or even in Miniopterus, there is, I think, undoubtedly a prenasal cartilage present in Notoryctes. It certainly cannot be called a prolongation anterior to the cartilaginous nasal septum, and since that in Notoryctes, extends right forwards to the end of the snout, it could not find room there. But it does split off from the ventral edge of the anterior part of this septum, and its hyaline nodule in position exactly corresponds to that found in the foetal calf. In part it also corresponds to the well-developed prenasal found in Miniopterus, since in each there is a central more or less fibrous ridge between the palatine processes of the premaxillae, giving off in Miniopterus, and to a certain degree in Notoryctes, a lateral sheet to support the papilla between Stenson's ducts, this latter somewhat resembling Marsupials, though in them the central ridge is absent. In Notoryctes, the prenasal is less developed than in Miniopterus, though exactly similar in relations to the surrounding cartilages and bones, because in the former the premaxillaries come together and fuse further back, and so shut out the possibility of the existence of any prenasal there, whereas in Miniopterus they do not meet in the middle line. One may here remember, also, that the nodule of hyaline cartilage, described by Klein in the Guinea-pig, supporting the papilla, is, as stated by Broom, probably to be regarded as a remnant of the lateral sheet of the prenasal cartilage.

VI.—Typically, in the Marsupialia there is to be found a single large vessel running along the outer face of the Organ. In Notoryctes we find two or three distinct vessels in this position, and a well-marked plexus in the median wall. In Polyprotodonts generally, this plexus is rudimentary, and in the lateral wall, in Diprotodonts, it is generally well marked, as also in the Edentates, while in the Rodents we often find a very large vascular plexus in this wall. Probably, as observed by Broom, this feature is not of much importance in classification, since in such closely allied forms as the Mouse and Guinea-pig, we find considerable differences. Similarly with the glands, though Broom has considered that the large vascular plexus, and the numerous glands present in Rodentia, point to an affinity with the lower Mammals. Further, he finds a great glandular development to be typical of large forms, *e.g.*, Lepus and Trichosurus. Here we have such in a small form. Here, doubtless, the numerous glands opening into the lumen of Jacobson's Organ are associated with the great amount of glandular material covering the septum, and the turbinal ridges, as is also the remarkable development of glands in connection with the degenerate eye : though I do not consider that, in the case of Jacobson's Organ, this great secretory power is necessarily developed at the expense of the sensory function, as in the eye—since we find in Jacobson's Organ here consistently with Broom's generalisation that the Organ is more highly developed in small forms than in large—it is in Notoryctes well developed, occupying fully two-thirds, and in parts the whole, of the cartilaginous trough in which it lies.

Conclusion.

It would seem then from the evidence of Jacobson's Organ, that we are justified in claiming for the Polyprotodont Notoryctes, that, while it still has traces of a Monotreme relationship, it shows a close affinity with the Diprotodonts by way of Aepyprymnus and Petaurus, and also, though at a much greater distance, with the Edentates and Rodents. It thus adds its measure of confirmation to the position given by Broom, as doubtful as yet, to the Rodentia in his classification of the Mammalian groups, in which he classes the Edentates and Rodents under one group, the Archaeorhinata. It, pari passu with this, adds its testimony to that of the muscular system, which has been held by Professor Wilson,[1] to show "enduring evidences of a real, if distant, morphological kinship" with that of the Edentates.

Part II.

Blood Vascular System.

This system, while not showing so far many special points having a general significance, has still a number of interesting conditions which are well worthy of record, in addition to the

1 Trans. Roy. Soc. S. Aus., 1894, p. 5.

normal conditions present. The study of the blood vessels, with the material at present obtainable, is not an easy matter, owing partly to the very brittle and absolutely bleached, and often quite transparent state of the vessels, and also to the great quantity of adipose tissue surrounding them, with a considerable admixture of strong fibres, which to the naked eye are often much more like ordinary blood vessels than are those vessels themselves. Recourse has frequently to be made therefore to the compound microscope and staining fluids for certainty of recognition. Especially is this so in the pectoral, abdominal, and pelvic regions. The following details involve observations made during a careful dissection of five individuals, aided by microscopic sections of one or two parts, such as the limbs.

The Heart.

The heart, which is normal in position, is somewhat more pointed than is often the case, the apex being well directed towards the left side, and separated dorsally from the diaphragm by a small lobe of the right lung, as in marsupials generally, its pericardium, however, being distinctly connected ventrally with the diaphragm, a condition not usual in marsupials. So far as can be seen there is no fossa ovalis on the auricular septum. In the left ventricle the mitral valve has two well-marked papillary muscles holding its chordae tendineae, one on the septum, the other on the outer wall, while the right auriculo-ventricular valve has three muscles corresponding to its three flaps. The right ventricle takes no share in the formation of the apex.

Pulmonary Circulation.

The main pulmonary artery is a short thick vessel arising from the right ventricle, and leaving the heart externally just behind the arch of the aorta. It divides almost immediately, and at a point directly ventral to the trachea, and anterior to its division, into the right and left pulmonary artery. The right branch is somewhat shorter and wider than the left, each of the branches lying ventral and somewhat anterior to the bronchus of its own side. Each artery divides at its entrance to the root of the lung into two main branches, the larger of which passes downwards to the lower part of the lung, alongside the main branch of the pulmonary vein.

The pulmonary veins are two large vessels, each of which is formed, as it leaves the lung of its own side, of two, or sometimes three, main vessels. The left pulmonary vein would appear to be both longer and wider, as also more sloping, than the right. The two unite and form a median trunk, as in Marsupials generally, similar in thickness to the corresponding trunk of the pulmonary artery, but at least twice as long as the latter. Each pulmonary vein runs ventral and also posterior to the bronchus of its own side. The division of the trachea into the bronchi occurs dorsal to the anterior half of this main pulmonary venous trunk. It then opens into the right auricle by a wide aperture, behind the emergence of the pulmonary arterial trunk, and in front and slightly to the right of the entrance of the left anterior vena cava into the right auricle. This is the usual arrangement of these parts in Marsupials.

Systemic Arteries.

The aorta emerges from the base of the heart at about the same level vertically, or slightly in front of the pulmonary artery, curving towards the front and left, round the trachea, and then backwards dorsally to the bronchus and root of the left lung. From the beginning of the arch, as usual, the coronary vessels are given off, one of which only can sometimes be seen with the unaided eye. The relative positions of the origins of the carotid and subclavian arteries vary somewhat in different individuals. The two types are : (1) The two carotid arteries, left and right, arise as a common trunk $\frac{1}{8}$-inch in length, from the root of which opens the right subelavian artery, the left subclavian leaving the arch considerably to the left end of the transverse part of this arch. This corresponds to the condition found in the majority of Marsupials and in Choeropus in particular.[1] (2) In other specimens again, and, so far as my material shows, most frequently, the right carotid and subclavian arteries arise as a common innominate trunk similar to that of many higher forms, including Man. The left carotid artery arises close to the base of this

1 Parsons : Jour. Linn. Soc. Lond., Zoology, vol. xxix., No. 188, Oct. 1903, p. 64.

innominate vessel, the left subclavian having its origin some little distance to the left of the left carotid artery, and not close beside it, as in Man. In this, Notoryctes resembles the broad-chested Marsupials, such as the Wombat and Koala.[1] Consequent on these variations the lengths of these vessels vary also. In relation to the nerves, the carotid artery lies ventral to the recurrent laryngeal, and pneumogastric nerves, crossing them obliquely as it runs outwards towards its anterior end. The sympathetic nerve appears to lie quite to the other side of the common carotid artery on each side. Where the two common carotids and the right subclavian artery are united at their origin from the aorta the pneumogastric also lies to the outer side of each common carotid, since the angle caused by this vessel in its course forwards is then considerably greater than where the vessels of the right side only are united to form an innominate vessel. The common carotid gives off no branches, but divides anteriorly into the external and internal carotids. The external carotid lies at first slightly below and distinctly nearer the median line than the internal carotid. It soon gives off the superior thyroid artery, which runs straight forwards and inwards to the thyroid gland. The ascending pharyngeal artery appears sometimes to be given off from the internal carotid just anterior to the bifurcation of of the common carotid, instead of being associated with the external carotid, as in higher forms. A little in front of the superior thyroid, the lingual artery is given off, running above the digastric and stylo-hyoid muscles, and continues under the mylo-hyoid muscles, giving off a branch to them, and then supplying the tongue and contiguous parts. Just where the lingual artery is given off, the external carotid turns outwards, curving round behind the masseter muscle. On its posterior side, as it curves round the articulation of the jaw, the external carotid gives off the occipital and posterior auricular arteries, while from its anterior side is given off the facial artery, the main vessel then breaking up into temporal and internal maxillary arteries. The four last mentioned arteries leave the main trunk very close together, the occipital arising about half way between these and the origin of the lingual artery. It will thus be seen that the

1 Owen : Anatomy of Vertebrates, vol. iii., p. 539.

lingual and facial arteries are much farther apart than is very often the case. Also, the facial here arises quite independently of the temporal artery as contrasted with Choeropus.[1]

The internal carotid, as previously stated, gives off immediately beyond its origin from the common carotid, the ascending pharyngeal artery, a condition to be contrasted with the normal origin of this artery from the external carotid trunk. This internal division of the carotid trunk runs down deeply, external at first to the external branch until it lies close alongside the pneumogastric nerve and the superior cervical ganglion, and passes forwards between the muscles to enter the skull.

The varying relations of the subclavian artery to the main aorta have already been described. The vertebral artery appears to be similar in position to that of other marsupials, but is generally very small, and often invisible. The inferior thyroid artery and its branches are, compared with their usual proportions, very slender, especially when contrasted with the internal mammary artery, which often approaches the main subclavian artery in size. The deep cervical and superior intercostal arteries leave the subclavian trunk separately, the latter being proximal to the former.

The long thoracic, posterior scapular and subscapular, are all normal in position but of considerable size.

The brachial artery divides early into ulnar and radial branches: the relative position of these to each other, and to the nerves and muscles of the forearm, conform in general to the usual mammalian type, as do also the branches and palmar arch of the large median ulnar artery, so far as they could be made out either by dissection or by sections. Here, as contrasted with the majority of marsupials, the ulnar branches pass over the condyle of the humerus instead of piercing it.

The thoracic aorta passes round dorsally to the left bronchus, and then posteriorly, in close contact with dorsal wall of the thorax, to which it gives off a few very small vessels, then piercing the diaphragm to enter the abdomen.

Abdominal aorta.—This gives off the coeliac artery, which is long and divides into well-marked gastric, splenic and

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1 Parsons: Jour. Linn. Soc. Lond., Zool., vol. xxix., No. 188, 1903, p. 64.

hepatic branches, and somewhat lower, a much larger vessel the superior mesenteric artery, which gives off a distinct inferior mesenteric artery to the lower parts of the intestine. Below these are the renal arteries (Fig. 8, *r.a.*), the right being small and short, the left long and broad. The spermatic arteries (*g.a.*) are very small. Near and posterior to the renal arteries, as so often in Marsupials, the aorta lies quite dorsal to the posterior vena cava, by which it is completely hidden, until some distance below its bifurcation, when the external iliac arteries come to lie, still somewhat dorsally but more to the outer side of the external iliac veins. From the following description it will be seen that there is a great difference between this region in Notorcytes and in the Marsupial type, in which the abdominal aorta, after giving off the external iliac arteries, continues back, giving off the two internal iliac arteries, the small continuation then forming the median sacral artery, *e.g.*, in the Kangaroo[1] and Choeropus.[2] In Notoryctes we find that the aorta bifurcates to form the common iliac arteries (*c.c.*), and in front of this bifurcation, from the dorsal wall of the aorta we may get a very small median sacral artery (*m.s.*), often only to be found by removing the neighbouring tissues, staining and examining them under the compound microscope. At other times I have found two, or in one case, three vessels, just visible to the naked eye, arising on either side, posteriorly, of the bifurcation, which from their distribution must represent the median sacral artery. At other times I was unable to detect any median sacral artery whatever. On its outer side each common iliac artery gives off what correspond in their distribution to the ilio-lumbar arteries (*i.l.*), and still further down there arises the circumflex (*c.*) artery, supplying the muscles of the abdominal wall, and the external circumflex (*e.c.*), a large vessel with ascending and descending branches supplying the muscles of the thigh. At about the middle of the thigh the external iliac or femoral artery divides into (1) the deep or profunda branch (*d.f.*), which sends off a large twig, apparently the superior perforating branch, to the muscles on the outer surface of the thigh, and (2) the superficial femoral (*s.f.*) to the muscles

1 Owen: Anatomy of Vertebrates, vol. iii., p. 540.

2 Parsons: Jour. Linn. Soc. Lond., vol. xxix., Oct, 1903, p. 64.

of the inner surface of the thigh and leg. The relations of these vessels in the leg and foot appear to be normal. On the inner surface of the common iliac artery and opposite to or above—but so far as my observations go, never below—the origin of the external circumflex, there is given off on each side, a very large internal iliac artery (*i.i.*). This is often as large as the external iliac artery. It sometimes arises almost dorsally from the common iliac artery, but whether so or not, always runs at first deeply and almost vertically upwards towards the dorsal surface of the animal, among the muscles of the pelvis. So sharply does it turn upwards, that, in dissecting from the ventral surface, it often appears to be absent, and is only to be seen on pushing over the main external iliac artery outwards. Often one side or the other has a much larger internal iliac artery than the opposite side, and, when this is the case, a small vessel can with care be seen connecting the two internal arteries. At first this artery gives off no branches, but then sends off a median sized one, probably the representative of the gluteal artery (*g.l.*) from its outer side. This branch appears to run almost vertically upwards to pierce the bony roof of the pelvis, and lose itself among the muscles of this dorsal region, including the "ischiotergal" slip. The internal iliac artery then passes backwards dorsally to the inner wall of the acetabulum giving rise on its outer face to two or three vessels, one of which is much larger than the others, which form by their anastomoses a plexus which is embedded in fatty tissue. From this plexus there arise two vessels running forwards and outwards to supply the muscles, ventral and lateral to the ankylosed metapophyses forming the dorsal wall of the pelvis. The largest and posterior of the three runs outwards and backwards (*s.c.*), and from its relations to the sciatic nerves, to the sacro-sciatic foramen, as well as its distribution to the muscles of the back of the thigh, probably corresponds to the sciatic artery of higher forms. The main trunk of the internal iliac artery passes directly backwards as the lateral sacral artery (*l.s.*), ventral to the transverse processes of the vertebrae, and supplies the pyriform and coccygeal muscles of this region. Just below the internal iliac artery there are given off two somewhat small vessels from the external iliac trunk, which correspond, the first with the superior vesical branch (*s.v.*) given off in Man from the internal iliac artery, and supplying the bladder and posterior end of the ureter, while the second (*i.v.*) sends a few twigs to the base of the bladder and passes on to give off branches to the testes and to the anal glands, as also to the fatty tissue in which they are embedded. In part, therefore, it corresponds with the inferior vesical artery of higher forms.

Systemic Veins.

The three venae cavae come into contact, as in Marsupials generally, just as they are about to open separately into the right auricle, on the dorsal surface of that chamber. The left anterior vena cava approaches the heart dorsally to the arch of the aorta, while the right runs back exterior to the exit of the aorta from the left ventricle, the opening of the pulmonary venous trunk being situated in the angle formed by the approximation of the two anterior venae cavae. In one specimen, so close together were the three openings of the venae cavae, that they formed practically one aperture, subdivided by the walls of the three confluent vessels.

So far I have not with certainty found the representatives of the inferior thyroid, vertebral and internal jugular branches.

External Jugular.

The temporo-maxillary vein brings back blood from the head and face, its posterior branch entering the external jugular vein, while its anterior branch receives blood from the muscles under the chin, and also by a submental and internal maxillary, and by a facial from the face. In one specimen it appeared as though there might be an anastomosis with an anterior jugular, but if so it was very ill-defined. The main external jugular trunk begins near the angle of the jaw, by the union of the posterior auricular and posterior part of the temporo-maxillary veins. It then crosses the sterno-mastoideus very obliquely, coming to lie external to it, near the clavicle dorsal to which it crosses. Just behind the ear it is joined by the posterior external jugular, a large vessel, and posterior to this by a considerable branch from the parotid gland and by the transverse cervical vein. On its inner side it receives two distinct branches from the submaxillary gland, these entering the external jugular vein just between the posterior external jugular and the parotid veins. Behind this, it receives the large suprascapular, bringing blood from the muscles of the shoulder and running alongside the clavicle.

Subclavian and Thoracic Veins.

The blood from the arms and axillae is returned by the representatives of the cephalic, basilic, vena comites, and subscapular veins, and, since these always seem to contain a considerable quantity of blood, the axillary vein is a large one. The blood is brought back from the thoracic walls and pectoral muscles by the usual vessels, of which the long thoracic vein is always large. The azygos veins are small, and not always easily found.

Abdominal Veins.

The posterior vena cava, anterior to its formation from the two common iliac veins, receives the lumbar veins, the two genital vessels, and two comparatively long and wide renal veins (Fig. 7, *r.v.*). Anteriorly it also receives a hepatic vein, which passes up dorsal to the digestive organs from both right and left main lobes of the liver, and enters the vena cava just as it pierces the diaphragm, a little to the right of the oesophagus. The portal vein is formed by the union of numerous branches from the mesentery of the small intestine, from the duodenal walls, pancreas and spleen, being joined by a large gastric vein close to its division into three parts one going to each of the two right lobes, and the other to the left lobe of the liver. [The bile and pancreatic ducts unite as they enter the wall of the duodenum, the duct so formed running obliquely through the wall to enter the cavity on a papilla]. The blood from the rectum is returned forwards by branches which unite to form the inferior mesenteric vein entering the hepatic portal vein. In one specimen (Fig. 7) on one side there was present, evidently as an abnormality, a second equally large and long renal vein (*R.V.*), which emerged from the kidney dorsal to the ureter, instead of ventral to it as does the normal vessel, and opened into the post caval vein, one-eighth of an inch behind the normal vessel. The spermatic vein (*g*) on each side leaves the testis running alongside the vas deferens (*v.d.*) to the root of the latter, when the blood vessel turns forwards, anastomosing by sometimes a double branch with a corresponding vein from the bladder (*v*). These two veins then run forwards along the ureter, until, when they reach the hinder edge of the kidney, they turn inwards (ventral to the abnormal renal vein when present), both entering the normal renal vein on the left side, while on the right the spermatic vein enters the right renal vein, and the vesical opens directly into the posterior vena cava. The blood from the hind limb is returned by the deep femoral and the superficial femoral veins, the former forming the external iliac vein, which receives a number of vessels from the muscles. Into it open the ilio-lumbar veins, two or three in number, the superficial and deep circumflex veins, and the long saphenous vein, all of which appear to have the same distribution and relative positions as in mammalia generally. The internal iliac veins are large and correspond very closely with the arteries in their branches and distribution, except that the well-marked vesical veins are branches of these internal iliac veins instead of belonging to the external iliac system, as do the corresponding arteries. Opening into the left internal iliac vein was occasionally a small but distinct median vessel bringing back blood from the testes and anal glands and from the surrounding fatty tissue.

Comparison with other Forms and Summary.

I regret that the literature obtainable here is somewhat scanty on the blood vascular system, so that I am not able to make as thorough a comparison as would otherwise be the case. The chief points of interest, however, are as follow :—

(1) The method of origin of the subclavian and carotid arteries from the aortic arch conforms in each of its two variations in Notoryctes, to one or other of the two marsupial types.[1]

(2) The blood vessels of the anterior limb are practically normal, except in size. They are larger than usual in Notoryctes, probably associated with the burrowing function of the fore-limb.

(3) In the Kangaroo and Vulpine Phalanger,[2] and also in

1 Owen : Comparative Anatomy of Vertebrates, vol. iii., p. 539.

2 *Loc. cit.*, pp. 538, 540-1.

Chaeropus,[1] we find the typical marsupial arrangement of two external iliac arteries arising from the abdominal aorta, which continues posteriorly as a common iliac trunk, ending in the median sacral artery. In Didelphys virginiana,[2] and in Vesperugo noctula,[3] and Ornithorhynchus,[4] we find an arrangement somewhat similar to that of Notoryctes, the internal iliac arteries coming off from the external iliac trunks. This also is found in the higher Mammals, of which the Rabbit and also Man may be given as examples. In many Marsupials, and also in some of the higher Mammals, *e.g.*, the Rabbit, there seem to be, so far as I can find to the contrary, a common internal iliac vein receiving an internal iliac branch on the right and left, and a median sacral vein ; thus in some specimens of Didelphys virginiana, McClure[5] finds this type, and also Hochstetter[6] in his series of Marsupial forms. In one species of Halmaturus, however, H. bennetti, Hochstetter finds a bifurcation of the postcaval vein into the two common iliac trunks, which are formed in turn by internal and external iliac veins, the common iliac receiving on the left side a median sacral vein. In some specimens of Didelphys virginiana,[7] McClure finds an approach to the Notoryctes type of internal iliac vein. Owen,[8] moreover, records a closely similar arrangement in the Ant-eaters and Armadilloes, and in some species of Bradypus. Each of these only differs from Notoryctes in that the latter has no median sacral vein, probably because of the small size of the tail, or the large size of the lateral sacral vessels. Except in Didelphys, in each of the Marsupial cases, so far as I can find any record, the arteries conform to the usual Marsupial type.

Conclusion.

If, with Owen,[9] we are to regard the state of development of the internal iliac vessels, especially the arteries, as a criterion

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1 Parsons: Jour. Linn. Soc. Lond., vol. xxix., 1903, p. 64.
2 McClure: Anat. Anz., 18, p. 444.
3 Hochstetter: Morphol. Jabrbuch., xx. bd. 4, Heft., p. 625.
4 Owen: Comp. Anatomy of Vertebrates, vol. iii., p. 538, 540-1.
5 McClure: Anat. Anzeiger, 18, p. 444.
6 Hochstetter: Morphol. Jahrbuch, xx. bd. 4, Heft., p. 626.
7 McClure. Anat, Anzeiger, 18, Figs. 4, 8. 15, 16.
8 Owen: Comp. Anat. of Vertebrates, vol. iii., pp. 542-4.
9 *Loc. cit.*, p. 541.

of the relationship of the particular animal to Monotreme or Eutherian sub-groups, we must certainly regard Notoryctes, with its large and important internal iliac arteries, as a highly developed member of the Marsupial group, thus corroborating what has already been found in dealing with Jacobson's Organ, namely, that there is an affinity between Notoryctes and the lower forms of Eutheria, distant though that relationship may be.[2]

DESCRIPTION OF PLATES VI.–IX.

REFERENCE LETTERS.

a.	Artery.
a.a.	Abdominal aorta.
a.c.	Alinasal cartilage.
bl.	Bladder.
c.	Circumflex artery.
c.c.	Common iliac artery.
c.t.	Cavernous tissue.
d.f.	Deep femoral artery.
e.c.	External circumflex artery.
e.p.	Epithelium lining palate.
e.s.	External surface of body.
f.p.c.	Fibrous papillary cartilage.
i.i.	Internal iliac artery.
i.l.	Ilio-lumbar artery.
i.s.r.	Inferior septal ridge.
i.v.	Inferior vesical artery.
g.	Spermatic vein.
g.d.	Spermatic artery.
gl.	Gluteal artery.
l.s.	Lateral sacral artery.
l.t.	Lymphoid tissue.
l.w.	Lateral wall of Jacobson's Organ.
m.b.	Maxillary bone.
m.g.	Mucous gland layer.
m.s.	Median sacral artery.
m.t.	Maxillo-turbinal bone.
m.w.	Mesial wall of Jacobson's Organ.
n.b.	Nasal bones.
n.c.	Nasal cavity.
n.f.	Nerve fibres.
n.f.c.	Nasal floor cartilage.
n.l.d.	Naso-lachrymal duct.
n.p.d.	Naso-palatine duct.
n.s.b.	Nasal septum (bone).
n.s.c.	Nasal septum (cartilage).
o.J.c.	Outer bar of Jacobson's cartilage.
ol.ep.	Olfactory epithelium.
p.b.	Premaxillary bones.
p.c.	Prenasal cartilage.

2 Since writing the above, a memoir by Dr. B. A. Bensley has appeared in the Transactions of the Linnean Society of London (Dec., 1903), on "The Evolution of the Australian Marsupialia," which, while confirming the close relationship of Notoryctes with the Phalangeridae, does not show any very close connection with the Macropodidae. nor is it easy from it to reconcile the resemblances to the American opposums in the blood vessels, with the emphasis laid by Owen on the evidence of the internal iliac vessels.

Reference Letters *(Continued).*

p.l.r.	Primary lateral ridge.	*sc.*	Sciatic artery.
p.p.p.	Palatine process of premaxillary bones.	*s.f.*	Superficial femoral artery.
		s.l.r.	Secondary lateral ridge.
p.p.s.	Shelf from palatine process.	*s.s.r.*	Superior septal ridge.
p.v.c.	Posterior vena cava.	*s.v.*	Superior vesical artery.
r.a.	Renal artery.	*ur.*	Ureter.
rc.	Rectum.	*v.*	Vein.
r.v.	Renal vein.	*v.d.*	Vas deferens
s.c.	Cartilage supporting naso-palatine canal.	*v.n.f.*	Ventral nasal furrow.

(All Figures were drawn by the aid of the Camera Lucida).

Figure 1.

Transverse vertical section through the anterior portion of the head of Notoryctes showing arrangement of cartilages forming nasal septum (*n.s.c.*), alinasals (*a.c.*), ventral processes from the septum (*n.f.c.*), and the prenasal cartilage (*p.c.*); also the premaxillary (*p.b.*) and nasal (*n.b.*) bones. The naso-lachrymal duct (*n.l.d.*) is seen passing through its canal immediately posterior to the union of the alinasals and the cartilages of the nasal floor (*n.f.c.*), to open into the ventral nasal furrow anteriorly. Zeiss A,* oc. 2.

Figure 2.

Ventral median portion of trsnsverse vertical section through head, a considerable distance behind Fig. 5, and just in front of Jacobson's Organ, to show swelling in Jacobson's cartilage (*J.c.*) which has, on the right side, quite lost its anterior connection with the nasal septum (*n.s.c.*), and on the left is just losing it. The naso-lachrymal duct is seen (*n.l.d.*) to lie in its groove in the alveolar process of the bone outside the outer nasal floor cartilages (*n.f.c.*). The ill-defined papillary cartilage (*f.p.c.*) is seen ventral to the palatine processes of the premaxillary bone (*p.p.p.*). Zeiss A,* oc. 4.

Figure 3.

Complied from two consecutive transverse vertical sections through Jacobson's Organ (*J.O.*) at the point where its duct

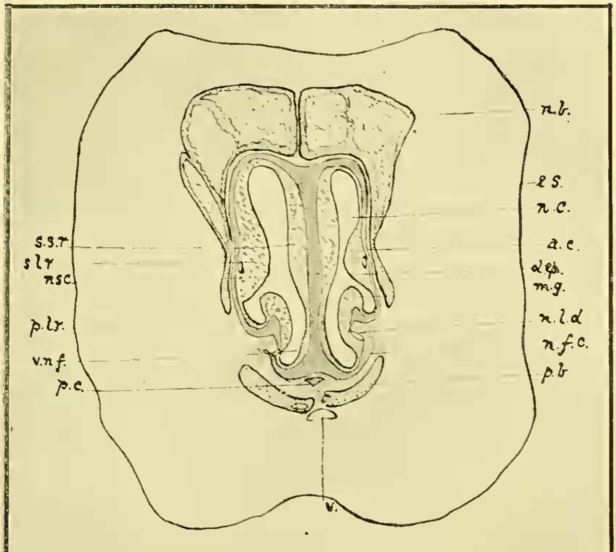
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FIG. 1.

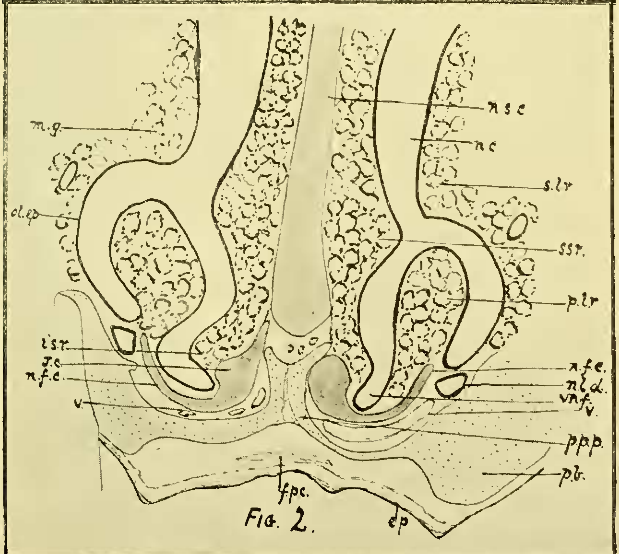
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FIG. 2.

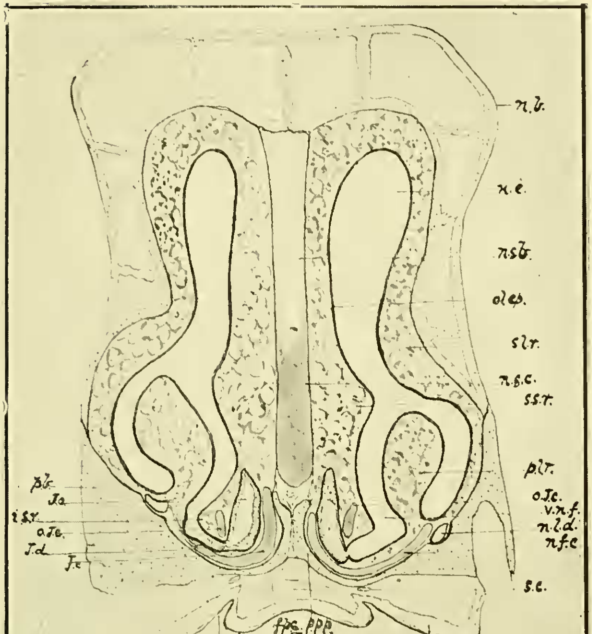
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Fig. 3.

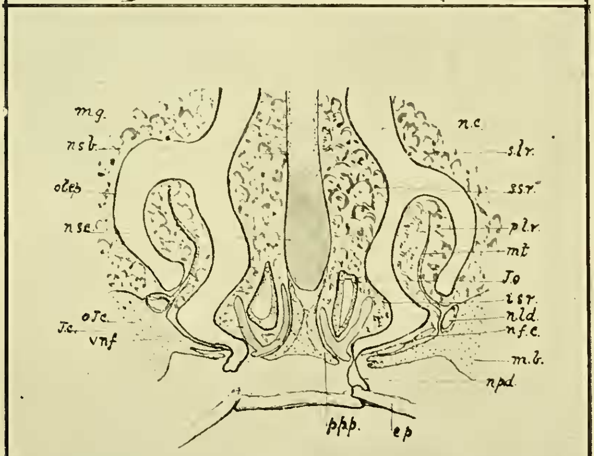
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Fig. 4.